Orthoptera in the early stages of post-arable rewilding in south-east England

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Abstract

The ideal aim of rewilding is to restore natural processes to create 'self-willed' ecosystems involving the creation of large areas of habitat subject to stochastic disturbance, connected by favorable corridors for species to disperse along. Reversion of arable farmland to grassland and scrub habitats on Black Bourn Valley nature reserve in Suffolk (south-east England) through non-intervention allowed succession to occur largely unmanaged. Fields in the early stages of rewilding (4–14 years) are found at Black Bourn Valley, while pond creation has been extensive since 2010, creating water edge habitat and heterogeneity to the re-establishing grassland. Monitoring of Orthoptera revealed statistical evidence that species diversity/richness and field grasshopper *Chorthippus brunneus* (Thunberg, 1815), meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821), common groundhopper *Tetrix undulata* (Sowerby, 1806) and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) were in higher abundance in fields ≥8 years since arable cropping ceased compared to those 4 years post reversion. Fields ≥8 years old were probably favorable due to the presence of microhabitats for basking and egg-laying orthopterans that included ant hills, sparsely vegetated pond edge and open swards with an abundance of fine-leaved grasses (*Agrostis* and *Festuca* spp.) and a low abundance of leaf litter. Lagomorph grazing by wild brown hare *Lepus europaeus* and rabbit *Oryctoloagus cuniculus* was critical in maintaining exposed soil for Orthoptera in the older fields, while deer paths appeared to create microhabitats that may be utilized by Orthoptera. We postulate that rewilding schemes on arable farmland should use a Rewilding Max approach and avoid the frequent usage of domestic livestock, relying on wild lagomorph and ungulate grazers to maintain an open mosaic habitat structure with only intermittent cattle, horse, or sheep grazing.

Keywords

Acrididae, biodiversity, bush-cricket, conservation, deer, grasshopper, Tettigoniidae, ungulate, wilding

Introduction

Orthoptera form an important part of grassland ecosystems across Europe (Köhler et al. 1987, Ingrisch and Köhler 1998, Humbert et al. 2009). Orders such as Orthoptera (grasshoppers, bush-crickets, and crickets) are an important component of invertebrate assemblages in agricultural ecosystems, particularly as prey for bird and spider species (Joern 1986, Belovsky and Slade 1993, Oedekoven and Joern 1998). Gardiner et al. (2002) suggest that intensively managed farmland habitats such as arable fields, heavily grazed improved pastures, and hay meadows have a low abundance of orthopteran species such as meadow grasshopper *Pseudochorthippus parallelus* (Zetterstedt, 1821) and field grasshopper *Chorthippus brunneus* (Thunberg, 1815). To reverse the decline of insects such as grasshoppers and bush crickets, rewilding of arable farmland may be highly beneficial.

The term rewilding was first used in North America in the 1980s (Noss 1985). Soulé and Noss (1998) proposed three key components of rewilding: large core protected areas, ecological connectivity, and keystone species that translated to the 3Cs of cores, corridors, and carnivores. Over time, Soulé and Noss's original concept has shifted into local interpretations but still incorporates self-regulatory ecosystems with minimal or no anthropogenic influence where wild grazers have a critical role (Dempsey 2021).

The role of wild herbivore grazers, such as lagomorphs (e.g., rabbit *Oryctoloagus cuniculus*) and ungulates (e.g., deer), in managing rewilded grasslands has not been studied in any depth with the aim of rewilding to recreate 'natural' ecosystems (Gordon et al. 2021b). Deer laydown areas and paths represent variation in sward height and could therefore be an influence on sward structure important for Orthoptera. Mixed approaches (e.g., relying on natural processes and introducing domestic grazers) with only minimal conservation intervention can be successful and may be necessary in some situations where non-intervention is not suitable (e.g., urban edge).

In recent times, the aim of rewilding in the UK has focused on restoring natural processes by creating large areas of habitat subject to stochastic disturbance connected by favorable corridors for species to disperse along (Carver and Convery 2021, Gordon et al. 2021a, b). Such ecological restoration on agricultural land that allows habitats to regenerate with a lack of active farmland (e.g., fertiliser application) or conservation management such as controlled livestock grazing is known as Rewilding Max (Gordon et al.

2021a,b). Domestic livestock (cattle, sheep, and ponies) are often used to graze rewilded farmland sites (e.g., Knepp Wildland in West Sussex, UK (Dempsey (2021)) after the initial establishment phase and grassland re-establishment (Casey et al. 2020). This form of conservation intervention without sole reliance on natural grazers is known as Rewilding Lite (Gordon et al. 2021b). However, introduced livestock can have detrimental impacts on Orthoptera where stocking density is too high and resultant sward height too short (Gardiner and Haines 2008). Across Europe, homogenously short swards established by overgrazing is the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016). The consequences of livestock grazing are largely influenced by the intensity of grazing, type of grazer, and rotational or seasonal aspects of the regime, which in turn have an impact on characteristics of grasslands, such as leaf litter development, plant species presence, sward height, and vegetation biomass (Marini et al. 2008, Fabriciusová et al. 2011, Fonderflick et al. 2014, Rada et al. 2014, Kurtogullari et al. 2020).

The abundance of Orthoptera, particularly grasshoppers, is strongly influenced by sward height, biomass, and the composition and the availability of bare earth (Clarke 1948, Gardiner et al. 2002). Increased herbage biomass and sward height through abandonment of grassland management on rewilded sites could lead to a concomitant decrease in sward temperatures and extinction of light near the soil surface, particularly where leaf litter is allowed to develop (Gardiner et al. 2005). This is an important factor in Orthoptera distribution, as Van Wingerden et al. (1992) suggest that the number of grasshopper species is reduced in such 'cold' grasslands due to slow egg development and delayed hatching, particularly where there is a dense leaf litter layer (Gardiner et al. 2005). In these tall and dense grasslands, the availability of bare earth for the basking and oviposition needs of Orthoptera is often provided by ant hills where eggs are laid and nymphs are found in spring (Richards and Waloff 1954). In European grasslands on abandoned arable land, some authors (e.g., King 2006, 2020, 2021) consider the yellow-meadow ant *Lasius flavus* to be a keystone species due to the bare earth habitat provided by its large mounds of earth.

Orthoptera are ideal for monitoring the effects of rewilding at sites due to established, easily repeated monitoring methods, speed of response to habitat change, and range of species with differing habitat requirements (e.g., bare earth, short grass, tall grass, and scrub species) (Gardiner et al. 2005). Using a simple acoustic and visual transect methodology accompanied by habitat measurements (e.g., sward height and bare earth), we would expect there to be a strong species-specific response to rewilding features (e.g., ant hills) and wild grazing. For example, *C. brunneus* may require the bare earth of ant hills for basking and oviposition, while common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) is a species of tall grassland that may benefit from an absence of lagomorph grazing (Marshall and Haes 1988).

The aim of this paper is to report on a study of the orthopteran assemblage of rewilded grassland on former arable farmland in Black Bourn Valley in Suffolk, UK. Results are discussed in relation to natural grazing pressure (brown hare, rabbit, and deer), grassland age since reversion commenced, and other factors such as sward height and bare earth habitat provided by ant hills and pond banks.

Materials and methods

Study site.—Black Bourn Valley has been owned and managed by Suffolk Wildlife Trust (SWT) since 1995 (it was formerly known as Grove Farm) in Suffolk, UK (52°15'0.4644"N, 0°51'1.422"E). The reserve is 119 ha in area and was previously intensively cropped for agriculture with nitrogen (N) fertilizer applied to a range of annual crops, including winter wheat. The Black Bourn River runs along the eastern edge of the reserve and is adjoined by riverside meadows (outside the scope of this study). The soil is a lime-rich loam and clay with slightly impeded drainage and moderate fertility. The farm had 11 farm ponds extant when SWT acquired the site in 1995. Nine new ponds have been created since 2010 as part of the Freshwater Habitats Trust's (FHT) Million Ponds Project. These ponds have several notably scarce and rare plants (e.g., tassel stonewort *Tolypella intricata*) for which the reserve has been designated a Flagship Pond Site by the FHT.

A total of eight fields were selected for this study due to their differing ages since reversion. Five fields were last plowed and cropped in 2017, two fields were last cropped in 2013, and one was cropped in 2007 (Fig. 1, Table 1). Once cropping ceased, all fields were allowed to naturally revert to grassland and scrub through succession with minimal intervention apart from mowing of footpaths and occasional light grazing (not on an annual basis). Throughout the duration of the 2021 summer study period, there was no active conservation management of any of the fields. A green lane ran through the site, and most fields were surrounded by scrubs or dense hedgerows. There were 10 ponds in the fields last cropped in 2013 or earlier (combined pond area 953 m^2) and six in the fields last cropped in 2017 (combined pond area 562 m^2). Most of the ponds had gently shelving banks (25–50° angle) and were sparsely vegetated.

Transect surveys.—A 1-m wide × 400-m long transect was established in all eight fields. Transects were arranged in a W shape (each arm 100 m) to ensure even coverage of each field and avoid any edge habitat effects. The transect method closely followed the methodology of Gardiner et al. (2005), Gardiner and Hill (2006), and Gardiner (2021). Each transect was walked at a slow, strolling pace (2 km/hr) on 3 occasions from May–August 2021. Adult individuals of all Orthoptera species along all transects were recorded acoustically and visually to determine assemblage composition and species diversity and richness.

Nymphs flushed from a 1-m wide band in front of the observer were recorded along all transects. As it is difficult to distinguish between species in the early instars (though not impossible, see Thommen 2021), numbers for nymphs of all species were lumped together for recording purposes. The surveys were undertaken in vegetation sufficiently short (<50 cm) to minimize the possibility of overlooking nymphs in tall grass or non-stridulating species such as groundhoppers (Tetrigidae) (Gardiner et al. 2005). With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006), although some species, such as long-winged conehead *Conocephalus fuscus* (Fabricius, 1793) and Roesel's bush-cricket *Roeseliana roeselii* (Hagenbach, 1822), are significantly under-recorded using visual transects (Gardiner and Hill 2006). A dual visual and acoustic monitoring method has been used by Weiss et al. (2013) to ensure complete coverage of the orthopteran fauna of sites. In the current study, a stridulation monitoring technique was used to record adult males of species that stridulated along the transects at the same time as visual monitoring by flushing. Stridulation monitoring has been used to record cryptic species in Essex and has been found to be effective compared to visual sighting transects and pitfall traps (Harvey and Gardiner 2006, Gardiner et al. 2010). Bat detectors were not required in the current study as the first author (TG) was able to reliably detect stridulating males up to 20 m away either side of the transect. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17°C).

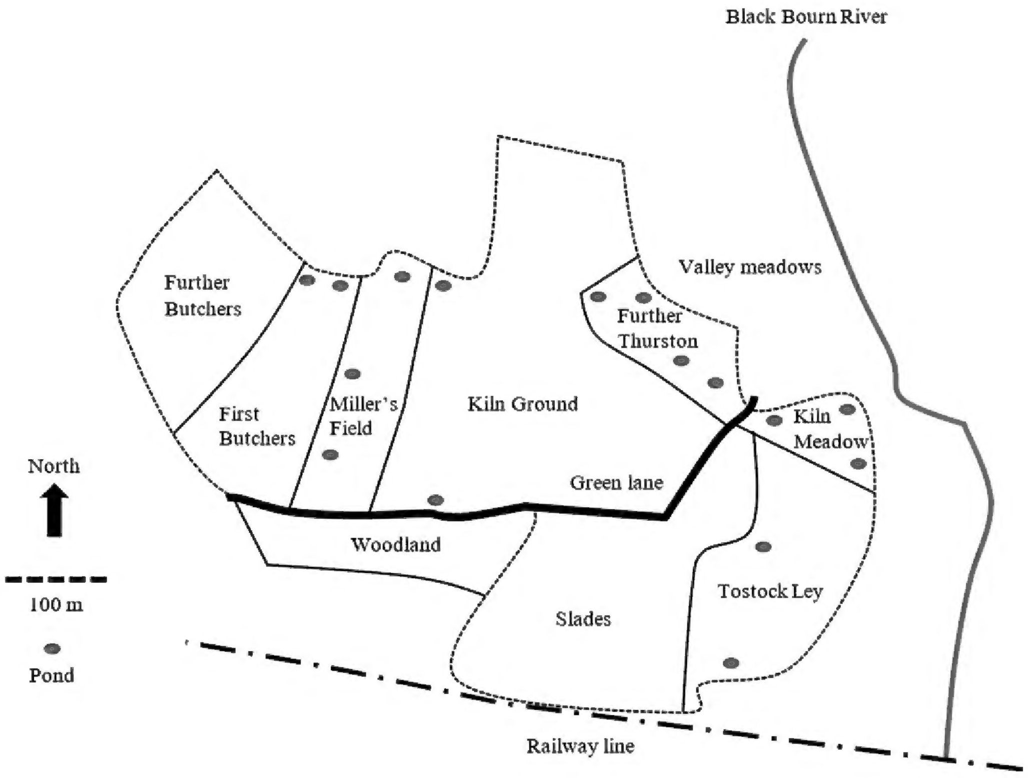

Fig. 1. Layout of the eight experimental fields at Black Bourn Valley with ponds and corridor habitats highlighted.

Table 1. Characteristics of the eight fields that had been taken out of arable cropping.

Field name	Area (ha)	Year since cropping ceased	Habitat on field perimeter	No. ponds	Pond areas (m^2)
Miller's Field	2.0	2007	H, GL	3	50, 80, 260
Further Thurston	2.1	2013	H, GL, M, W	4	80, 72, 98, 138
Kiln Meadow	1.6	2013	H, GL, W	3	32, 50, 140
Tostock Ley	4.4	2017	H	2	85, 90
Kiln Ground	14.7	2017	H, GL, M	2	35, 50
First Butchers	3.0	2017	H, GL	2	125, 130
Further Butchers	5.4	2017	H	0	-
Slades	5.7	2017	H, GL, R	0	-

Key: H = hedge, GL = green lane, M = marsh, R = railway bank, W = woodland

Natural grazing pressure and habitat characteristics surveys.—A total of 40 sward heights were recorded at random positions along the Orthoptera transects using a 1-m rule for each of the eight fields in early September 2021. In each field, ant hills were counted along the 400 m long Orthoptera transects in a 1-m wide band; additionally, the number of individual wild lagomorph (differences between brown hare and rabbit were not determined, so droppings pooled for both species) droppings (dung balls) were recorded in the same 1-m band to ascertain the level of grazing pressure in the fields (Wood 1988, Gibb and Fitzgerald 1998, Millett and Edmondson 2013).

Four of the six British ungulate species have been recorded at Black Bourn Valley: fallow deer *Dama dama*, muntjac *Muntiacus reevesi*, red deer *Cervus elaphus,* and roe deer *Capreolus capreolus*. Due to the known presence of ungulates on site, individual deer pellets (not classified to species) were counted along a 5-m wide × 200-m long transect in each field in October 2021 when the vegetation had died back, allowing easy sighting of fecal matter. The counting of deer droppings (droppings of all species lumped together for analysis) followed the methods of Marques et al. (2001). In addition to the dropping counts, deer laydown areas (flattened areas of grass at least 2 × 2-m in area) and deer paths (parted grass through vegetation) were recorded where they were observed within the 5 × 200-m transect in each field.

In the fields where arable cropping ceased in 2017 and in 2013 or 2007, 2 × 2-m quadrats were randomly surveyed (11 and 7 quadrats, respectively) to collect vegetation data. The number of quadrats surveyed in both field types was approximately proportionate to the number of fields studied in each (i.e., 5/8 fields for 2013 or 2007 = 63%, 11/18 quadrats = 61%). Each plant species recorded in a quadrat, along with bare earth and leaf litter (dead and decaying vegetative material, typically grass in this study), was given a DOMIN value in accordance with National Vegetation Classification survey methods (Rodwell 2006). The DOMIN scale assigns percentage cover of species or habitat features to a numeric grade using the following scale: 1, <4% few individuals; 2, <4% several individuals; 3, <4% many individuals; 4, 4–10%; 5, 11–25%; 6, 26–33%; 7, 34–50%; 8, 51–75%; 9, 76–90%; 10, 91–100% (Rodwell 2006).

Statistical analysis

Orthoptera.—For data analysis, two age classes for the fields were used: 1) fields where arable cropping ceased in 2017 (5 fields) or 2) in 2013 or 2007 (3 fields). This represented either 4-year-old reversion or ≥8 years, since arable cropping terminated. All detections of Orthoptera (visual or acoustic) were summed for each field for the survey period (3 surveys) to determine the relative abundance of adults of each species and nymphs in accordance with previous studies (notably, Weiss et al. 2013). Independence of transects was assumed, and data was pooled for each one in a similar way to data analysis in other monitoring studies (Nur et al. 1999).

Species richness was calculated for each field. Assemblage diversity estimates were also calculated using Version 4.1.2. Species Diversity and Richness software (Pisces Conservation Ltd, IRC House, The Square, Pennington, Lymington, Hampshire) from data collated from each of the two methods. The Shannon-Wiener Diversity Index (H′, Kent and Coker 1992) was calculated using the total number of adult individuals recorded for each Orthoptera species in each field. All data were square-root transformed to correct for non-normality before analysis (Heath 1995).

To determine whether species richness and diversity and the abundance of adults (of all species) and nymphs differed between fields 4 years and 8 or more years since arable reversion began, a Student's t-test was used for all comparisons. The mean abundance of the most abundant species/field was also compared between the two field types. Corrections were made for unequal variance where necessary using Satterthwaite's approximate t-test, which is a method in the Behrens-Welch family (Armitage and Berry 1994, Heath 1995). Significance was accepted as evidence based on the following scale in accordance with Muff et al. in press: p-value >0.1, little or no evidence; 0.05–0.1, weak evidence; <0.05, moderate evidence; <0.01, strong evidence; or <0.001, very strong evidence.

Natural grazing pressure and habitat characteristics surveys.—The counts of ant hills, lagomorph droppings (brown hare and rabbit pooled), deer droppings (all species combined), laydown areas, and paths were individually summed for each field, and along with DOMIN values for bare earth, leaf litter, the five most abundant plant species, bryophytes and plant species richness, data were square-root transformed to correct for non-normality (Heath 1995). To determine whether all of these variables differed between fields 4 years old and those 8 or more years post-arable reversion, a Student's t-test was used in each case with corrections made for unequal variance where necessary using Satterthwaite's approximate t-test (Armitage and Berry 1994, Heath 1995).

Results

Nine species of Orthoptera were recorded on the Black Bourn Valley reserve, including three species uncommon in this area of Suffolk (Table 2). The most commonly recorded species were *P. parallelus* (21% of adult detections) and *R. roeselii* (20%), followed by *C. fuscus* (19%) and *C. brunneus* (12%). Less common species included *O. viridulus* and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) (10% each). The common groundhopper *Tetrix undulata* (Sowerby, 1806) and lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer, 1773) were found in much lower abundance (3%), while the dark bush cricket *Pholidoptera griseoaptera* (De Geer, 1773) was a rarity (1%).

The abundance of 6 of the 9 species (*C. albomarginatus*, *C. brunneus*, *O. viridulus*, *P. parallelus*, *T. subulata*, and *T. undulata*) was highest in one field (Kiln Meadow, cropping ceased 2013; Figs 1, 7) where 30% of the total detections of adult Orthoptera were recorded. For *O. viridulus*, *T. subulata*, and *T. undulata*, a very high percentage of the total recorded adults for each species were from Kiln Meadow and Further Thurston combined (82%, 89%, and 73%, respectively). For *P. griseoaptera*, 83% of adults were recorded from Miller's Field (cropping ceased in 2007).

There was very strong evidence ($p < 0.001$) that species richness and diversity and the abundance of *T. undulata* were significantly higher in fields ≥8 years since cropping cessation compared to those only 4 years since cropping ceased (Table 2). There was moderate evidence ($p < 0.05$) that *C. brunneus* and *P. parallelus* were significantly more abundant in fields ≥8 years old and only weak evidence ($p < 0.10$) for *T. subulata* (Table 2). Very strong evidence ($p < 0.001$) indicated that the most abundant species (% of total number) in each field was significantly higher in the younger fields (c. 43%) compared to the older fields (c. 22%). In 4 out of the 5 fields 4 years post-cropping, *C. fuscus* was the most abundant orthopteran, comprising c. 43% of the total number of Orthoptera overall across the 5 younger fields. In 2 out of the 3 older fields (≥8 years post-cropping), *P. parallelus* was the most abundant species, forming 20.6% of overall sightings. In these older fields, *C. fuscus* comprised only 11.3% of adults.

Table 2. Mean number of Orthoptera nymphs and adults of each species and species diversity and richness in fields 4 and ≥8 years since cropping cessation, significance evidence shown (Student's t-test).

Species	4 years		≥8 years		t value	p	Evidence
Pseudochorthippus parallelus	12.8	± 1.9	36.0	± 11.0	-3.32	0.02	Moderate
Chorthippus brunneus	8.2	± 1.8	23.3	± 3.9	-3.59	0.01	Moderate
Roeseliana roeselii	11.2	± 1.9	28.0	± 11.0	-1.28	0.33	None
Chorthippus albomarginatus	1.6	± 0.5	4.7	± 3.2	-1.23	0.26	None
Conocephalus fuscus	28.4	± 5.6	19.7	± 4.1	1.07	0.33	None
Pholidoptera griseoaptera	0.2	± 0.2	3.7	± 3.2	-1.24	0.34	None
Omocestus viridulus	2.0	± 0.6	26.0	± 11.0	-2.74	0.11	None
Tetrix subulata	0.8	± 0.6	26.0	± 11.6	-3.05	0.09	Weak
Tetrix undulata	0.0	± 0.0	7.3	± 0.9	-15.12	<0.001	Very strong
Nymphs (all species)	38.6	± 16.3	61.0	± 20.4	-0.94	0.38	None
Most abundant species (%)	42.9	± 3.8	22.2	± 1.8	4.40	<0.001	Very strong
Species richness	6.2	± 0.4	8.7	± 0.3	-4.44	<0.001	Very strong
Species diversity	1.5	± 0.1	1.9	± 0.0	-6.32	<0.001	Very strong

There was moderate evidence ($p < 0.05$) that ant hill density, lagomorph droppings, and the number of ponds were significantly higher in fields ≥8 years since cropping cessation (Table 3). Contrastingly, there was very strong evidence ($p < 0.001$) that leaf litter was significantly less abundant in fields ≥8 years since cropping cessation. Only weak evidence was obtained that there was a higher number of deer paths in the older fields ($p < 0.10$).

Of the five most abundant plant species, two were significantly more numerous in fields ≥8 years since cropping cessation: creeping bent *Agrostis stolonifera* (moderate evidence) and red fescue *Festuca rubra* (very strong evidence; Table 4). Overall plant species richness was also significantly higher (very strong evidence) in the older fields (Table 4). In contrast, soft brome *Bromus hordeaceus* was more abundant in fields 4 years post-cropping (strong evidence). Two species, Yorkshire fog *Holcus lanatus* and bristly oxtongue *Helminthotheca echioides*, had similar abundance in both types of field, as did bryophytes (Table 4).

Discussion

Species richness and abundance in a regional context

The total of 9 species recorded at Black Bourn Valley is supplemented by species not observed on the transects, which include the oak bush-cricket *Meconema thalassinum* (De Geer, 1773) and speckled bush-cricket *Leptophyes punctatissima* (Bosc, 1792). *Omocestus viridulus* was relatively abundant, but is a scarce species in central Suffolk (Ling 2000), while the two *Tetrix* groundhoppers are local to the county. On intensively managed arable farmland in south-east England, *O. viridulus* is almost never found (Gardiner 2010b), while groundhoppers such as *T. subulata* are occasionally observed in low numbers along field edge footpaths (Gardiner 2007). The presence of *O. viridulus* in fields 4 and ≥8 years since cessation of arable cropping suggests that this species was quick to establish populations despite an allegedly slow colonization rate of new grasslands and apparent restriction to unimproved grassland (Gardiner 2010b).

The overall density of grasshoppers (234 adults/ha) compares favourably with intensively managed farmland (<100 adults/ha; Gardiner et al. 2002), indicating that rewilding arable land can successfully promote large insect populations in the early stages of reversion to grassland and scrub.

Factors influencing the colonization of rewilded fields

Pond edge.—Pond edge habitat with bryophytes (moss cover) and bare earth established by digging and grazing lagomorphs may be important for *T. undulata* and to a lesser extent *T. subulata* in fields ≥8 years since cropping cessation where there were small farm ponds, particularly those created since 2010, or restored old waterbodies (Fig. 2). Both *Tetrix* groundhoppers were found to occur around the ponds in this study, although this may cause issues with reproductive interference (Hochkirch et al. 2008). Both groundhoppers can be abundant in river valleys such as the Bourn, where they require both sparsely vegetated ground and tall vegetation in close proximity to prevent individuals being washed away during floods (Musiolek and Kočárek 2017). Groundhoppers typically utilize micro-habitats in close proximity and can match their color morph to the substrate for camouflage (Forsman 2000, Ahnesjö and Forsman 2006, Forsman et al. 2011). In this way, melanic forms can be abundant on burned ground or where soil is darker around silty river valley ponds.

Fig. 2. Pond edge habitat with exposed soil in rewilded fields at Black Bourn Valley, valuable for groundhoppers (*Tetrix* spp.) and field grasshopper *Chorthippus brunneus*. Photo credit: Tim Gardiner.

The importance of restoring old ponds by vegetation clearance and creating new ones should be recognized in proposals for rewilding at new sites to benefit orthopterans that require bare earth edges clear of vegetation by lagomorph grazing (Fig. 2).

Ant hills.—To determine why arable reversion to grassland affects Orthoptera, the habitat preferences of species should be examined. Habitat preferences of Orthoptera may relate to the choice of oviposition site, food preferences, vegetation height, and grassland management regimes (Clarke 1948, Gardiner 2006, 2009). Waloff (1950) stated that *C. brunneus* and *P. parallelus* lay their egg pods in the superficial layers of the soil. Bare earth, often on ant hills, is the usual egg-laying site for *P. parallelus*, although this species and *O. viridulus* have been found to oviposit into grass-covered soil (Waloff 1950). Exposed soil on ant hills may offer other benefits for grasshoppers by providing sites where they can bask (Key 2000), as it is often much warmer than surrounding vegetation (Fig. 3). Although bare earth overall did not vary between field types, there were greater numbers of ant hills in fields ≥8 years since cropping cessation, which indicates that micro-heterogeneity in unvegetated habitats may be important for egg-laying and basking *P. parallelus* and *C. brunneus,* which were in higher abundance in the older fields (Table 2). Nymphs were evenly distributed between field types, perhaps reflecting the need for a diversity of resources including bare earth, but also heterogeneity in sward structure, which was similar in both. Early instar grasshopper nymphs of *C. brunneus* and *P. parallelus* are often found in short grassland near oviposition sites before moving to taller swards (10–20 cm height) as they mature (Gardiner et al. 2002). Adults may then return to bare earth and sparse sward patches, such as those established by ant hills or rabbit grazing.

Ant hills in the older fields may have acted as hot 'sun traps' favorable for Orthoptera (Gardiner and Dover 2008, Voisin 1990), particularly species such as *C. brunneus* and *P. Parallelus,* which were in high abundance in those field types where overall species diversity and richness were also high (Table 2).

As succession progresses on rewilded sites, the prevalence of ant hills should be monitored to ensure that this valuable resource for invertebrates persists. If there is a loss of bare earth on ant hills over time, then site managers could consider periodic rotovation of strips through fields for early successional, disturbance-dependent species (e.g., *C. brunneus* and groundhoppers), similar to the management of nearby Breckland heaths (Gardiner 2020). Any rotovation should be irregularly undertaken to avoid too much intervention in natural processes, akin to Rewilding Max. However, a brownfield-type open mosaic habitat with patchy bare earth may only be possible on poor or moderately fertile soils.

Fig. 3. Ant hill (*Lasius* spp.) in rewilded grassland at Black Bourn Valley, probably used for egg-laying and basking by grasshoppers. Photo credit: Tim Gardiner.

Lagomorph grazing.—The aim of Rewilding Max to reinstate natural processes ideally means an absence of introduced livestock, such as cattle, horses, or sheep, relying on wild grazing animals where possible to manage succession. However, at several rewilded sites, livestock has been introduced to control natural processes (Rewilding Lite), while wild grazers, such as lagomorphs and ungulates, have a reduced influence. There is little information on how successful wild grazing animals are in maintaining grasslands in the absence of domestic livestock on rewilded sites.

Wild grazing animals play a significant part in reducing vegetation height and cover (Gardiner 2018, Fargeaud and Gardiner 2018). On sea wall pollinator strips, wild rabbit grazing had a significant impact on sward height and the density of *R. roeselii* adults and orthopteran nymphs (Gardiner and Fargeaud 2020). Rabbits grazed the closed grassland, reducing grass growth and creating patches of exposed soil though their burrowing activities that were favorable for basking nymphs (Gardiner et al. 2002).

Clarke (1948) suggested that excessive grazing by rabbits promotes sparser vegetation comprised of less vigorous grass species (such as sheep's fescue *Festuca ovina*) which is consequently more favorable to grasshoppers, perhaps because of the open sward structure and warmer microclimate (Gardiner and Hassall 2009). It is important to remember that microclimate may be crucial in providing warm temperatures for the development of large Orthoptera populations (Marshall and Haes 1988), particularly in rewilded fields where leaf litter is reduced ≥8 years since cropping cessation allowing greater penetration of solar radiation to the soil surface.

Ant hills and pond edges may assume greater importance in a sward managed only by wild grazers (e.g., brown hares and rabbits). The lagomorph grazing at Black Bourn Valley is mainly assumed to be by brown hares, although some rabbit droppings were located around the ponds where there were bare earth patches (Fig. 2).

Short sward patches established by lagomorph grazing, particularly when allied to sloping pond banks and ant hills, will have excessively hot temperatures (>40°C), similar to hay meadows after cutting (Gardiner and Hassall 2009), which are unlikely to be favored by grasshoppers in the absence of 'cool' tussocks in close proximity. Both field types had mean sward heights >30 cm, which could provide grasshoppers with numerous sheltered 'cool' areas of tall vegetation away from ant hills and pond edges where temperatures may be excessively hot during summer. This behavioral thermoregulation may account for the persistence of species such as *C. brunneus*, *P. parallelus,* and *T. undulata* in fields ≥8 years since cropping cessation where ant hills and sparsely vegetated pond edges (basking and egg-laying sites) were frequently in close proximity to cooler tall vegetation for shade-seeking orthopterans (Fig. 2).

Intensive grazing by unmanaged wild rabbit populations in Epping Forest in the UK led to the extirpation of *O. viridulus*, a grasshopper with a preference for tall grassland (Gardiner 2010b). Rabbits also reduce the abundance of *O. viridulus* through the creation of uniformly short swards with little cover from avian predation and excessively hot microclimates (Gardiner 2021). Therefore, uncontrolled rabbit grazing could pose a threat to *O. viridulus* on heavily grazed areas of rewilded sites. The extent to which rabbits influence the favorability of rewilded grasslands for insect orders such as Orthoptera should be a focus of further research on arable reversion sites.

Table 3. Natural grazing and habitat variables for fields 4 and ≥8 years since cropping cessation; Student's t values and significance evidence shown for differences between means in each row.

Variable	4 years		≥8 years		t value	p	Evidence
Ant hills/field	7.2	± 2.7	40.3	± 18.8	-2.53	0.04	Moderate
Bare earth (mean DOMIN)/quadrat	4.5	± 0.8	3.4	± 0.8	0.74	0.47	None
Deer droppings/field	4.4	± 2.2	3.7	± 2.3	0.20	0.85	None
Deer laydown areas/field	16.2	± 6.3	8.7	± 3.9	0.95	0.38	None
Deer paths/field	33.2	± 3.5	45.3	± 3.8	-2.29	0.06	Weak
Lagomorph droppings/m^2	0.5	± 0.4	3.5	± 0.9	-3.60	0.01	Moderate
Leaf litter (mean DOMIN)/quadrat	4.3	± 0.8	1.0	± 0.8	5.29	0.001	Very strong
No. ponds/field	1.2	± 0.5	3.3	± 0.3	-2.69	0.04	Moderate
Sward height (cm) range/field	83.6	± 9.6	85.0	± 3.2	-0.24	0.82	None
Sward height (cm)/field	44.1	± 5.6	31.4	± 3.5	1.64	0.15	None

The main source of error in this study may be the accuracy of the lagomorph dropping counts. Droppings may have been easier to locate in shorter, lagomorph-grazed vegetation and would have dried and been less likely to decay in such situations compared to the taller and moister vegetation present in some fields. Therefore, the lagomorph dropping counts must be viewed with some caution, and further studies should be undertaken.

Plant species changes and sward height.—Changes in plant species composition may have been a key influence on the abundance of *C. brunneus* and *P. parallelus* in fields ≥8 years since cropping cessation where fine-leaved grasses, *A. stolonifera* and *F. rubra*, were in higher abundance (Table 4, Fig. 4). The development of open sward structure with *Festuca* and *Agrostis* grasses in the older field types benefits these two grasshopper species that require a shorter sward composed of fine-leaved grass species (Gardiner et al. 2002). While neither field type offered the optimal mean sward height for *C. brunneus* and *P. parallelus* of 10–20 cm, the presence of diversity in sward structure in fields 4 and ≥8 years since cropping cessation indicates that patchy habitat was present with shorter swards for grasshoppers (Fig. 4). It also suggests that microhabitats, such as ant hills and pond edges, may assume greater importance in a sward managed only by wild grazers (e.g., brown hares and rabbits). The lagomorph grazing at Black Bourn Valley is mainly assumed to be by brown hares, although some rabbit droppings were located around the ponds where there were bare earth patches (Fig. 2).

Short 'hot' sward patches established by lagomorph grazing are unlikely to be favorable for grasshoppers in the absence of 'cool' tussocks in close proximity. Both field types had a mean sward height >30 cm, which will have provided grasshoppers with numerous sheltered 'cool' areas of tall vegetation away from ant hills and pond edges where temperatures may be excessively hot.

Ungulate grazing.—Wild ungulates are browsers that consume grasses, sedges, shrubs, and trees (Uresk and Dietz 2018). However, the influence of deer grazing on swards was assumed to be minimal at Black Bourn Valley (Table 3), despite the positive (Adler and Proud 2021) and negative (Gardiner 2011) influence it can have elsewhere.

In subalpine pastures in the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois). However, they did observe the small-scale alteration of habitats and plant N content by ungulates, which in turn affected Orthoptera abundance and diversity. Gardiner (2011) noted a reduced species richness of Orthoptera in red deer-grazed enclosures near Broadway Tower in the Cotswolds, UK, where sward height was mainly 5–10 cm with only occasional ungrazed taller vegetation (Gardiner 2011).

Table 4. Mean DOMIN abundance data/field for five most abundant plant species, bryophytes (mosses, liverworts and hornworts) and species richness for fields 4 and ≥8 years since cropping cessation, significance evidence shown (Student's t-test).

Species/family	4 years		≥8 years		t value	p	Evidence
Helminthotheca echioides	4.9	± 1.0	2.3	± 0.5	1.43	0.17	None
Agrostis stolonifera	1.0	± 0.8	3.4	± 0.5	-2.77	0.02	Moderate
Bromus hordeaceus	3.8	± 0.7	0.6	± 0.3	3.65	0.002	Strong
Holcus lanatus	2.9	± 0.9	1.9	± 0.4	-0.02	0.98	None
Festuca rubra	0.6	± 0.5	3.9	± 0.4	-7.05	<0.001	Very strong
Bryophytes	4.8	± 0.4	4.0	± 0.8	1.16	0.29	None
Species richness	13.7	± 1.0	28.3	± 1.1	-4.93	<0.001	Very strong

Fig. 4. Rewilded grassland at 4 years (right) and ≥8 years (left) since cropping cessation. Note the greener vegetation of the soft brome *Bromus hordeaceus*-dominated field (right) compared to the red and brown hues of the creeping bent *Agrostis stolonifera* and red fescue *Festuca rubra* of the older fields. Photo credit: Tim Gardiner.

Deer droppings and laydown areas were not significantly different between field types in the current study, indicating that ungulate grazing was evenly distributed across Black Bourn Valley (Fig. 5). There was weak evidence of greater deer path frequency in older fields (Fig. 6), indicating that ungulate passage may have had localized benefits for grasshoppers that need heterogeneity in sward structure. However, the shorter grass of deer paths was not numerous enough to make a difference to either mean sward height or structural range (Table 4), despite the micro-habitat mosaic and structural diversity that has been observed in other studies (Adler and Proud 2021). Deer may control the regrowth of scrub in the long term to maintain the mosaic of sparse grassland and woody vegetation, while ants and lagomorphs create the necessary bare earth for disturbance-dependent invertebrates. Seed dispersal can also occur due to ingested seeds being deposited across fields in fecal matter from grazing deer and lagomorphs, which may lead to the establishment of *A. stolonifera* swards (Eycott et al. 2007). It is possible that *A. stolonifera* swards favorable for *C. brunneus* and *P. parallelus* have developed along this successional trajectory at Black Bourn Valley.

Unstudied factors influencing colonization

Corridor linkage.—The presence of an ancient green lane corridor with hedgerows and grass margins may have allowed *O. viridulus* to spread quickly into the rewilded fields (Fig. 7). The main population of *O. viridulus* appeared to be centered in two of the older fields where cropping ceased in 2013, from which individuals probably colonized the fields taken out of cropping in 2017. Both fields with high concentrations of *O. viridulus* are located next to a species-rich unimproved meadow and the Black Bourn River Valley, which may have been sources of colonizing grasshoppers and likely explains the fast colonization into rewilded fields (it was present in 7 out of the 8 fields). In the field nearest to Black Bourn River (Kiln Meadow; 100 m), 5 out of 8 of the remaining species were in highest abundance, further highlighting the benefits of connectivity between rewilded fields and corridors to aid quick colonization.

Fig. 5. Deer laydown areas with shorter vegetation (and droppings), creating localized variation in sward structure in both field types. Photo credit: Tim Gardiner.

Range-expanding species such as *C. albomarginatus*, *C. fuscus*, and *R. roeselii*, which are spreading rapidly due to climate change (Gardiner et al. 2002, Gardiner 2009), were early colonizers of fields, being in similar abundance in fields 4 and ≥8 years since cropping cessation (Table 2). These pioneer species benefit from unmanaged grasslands and can build up large populations in such habitats on farmland in the UK (Gardiner et al. 2002, Gardiner 2009). *Conocephalus fuscus* formed just over 40% of the orthopterans counted in fields 4 years since cropping cessation, falling to c. 11% in those ≥8 years since cropping cessation, where *P. parallelus* was the most abundant species.

Scrub development.—In the oldest field (Miller's Field, 2007), which had well-developed scrub patches, *P. griseoaptera* was in its highest abundance, reflecting a well-documented preference for woody habitats (Marshall and Haes 1988). It should also be remembered that patches of scrub are desirable for red-list declining birds such as turtle dove *Streptopelia turtur* and common nightingale *Luscinia megarhynchos*, both of which were recorded in the two rewilded fields where cropping ceased in 2013 (Further Thurston and Kiln Meadow) at Black Bourn Valley. Therefore, light scrub encroachment is desirable from a conservation viewpoint, particularly as it also supports orthopterans such as *L. punctatissima* and *M. thalassinum*, both of which can spread from green lanes into adjacent habitats (Gardiner 2010a). A beating survey of the hedgerows and woodland would reveal the distribution of arboreal bush crickets across the rewilded area.

Fig. 6. Deer paths through tall grassland, creating localized variation in sward structure in older fields. Photo credit: Tim Gardiner.

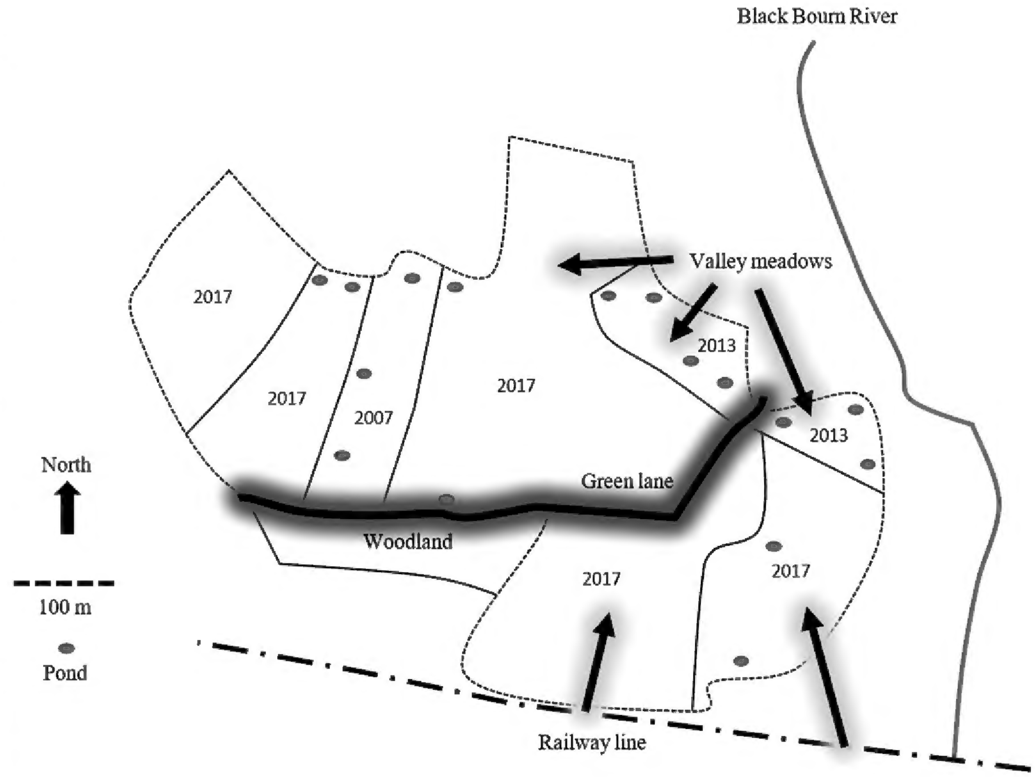

Fig. 7. Layout of the eight experimental fields at Black Bourn Valley (year since cropping cessation shown) showing the likely dispersal corridors onto rewilded farmland and the main green lane corridor, which may have acted as a green highway to fields at greater distance from the river valley corridor.

Soil fertility.—On soils with high fertility (e.g., clay) farmed intensively for years, a low diversity, tussocky sward less favorable to Orthoptera may develop (Gardiner 2006, 2009). Natural regeneration on highly fertile arable soils often produces grassy swards of low diversity with minimal benefits to Orthoptera due to unfavorable tall sward height and lack of structural diversity (Gardiner 2009) or to butterflies that are restricted because of the dearth of nectar sources (Field et al. 2005, 2006, 2007). Therefore, farmland suitable for the maximal rewilding benefits must be carefully chosen. Farmers could remove fields from arable production and rewild them on the infertile or difficult-to-crop parts of their farms, perhaps rewilding 10–15% of total crop area. Rewilding Max may be the preferred option in these circumstances for Orthoptera, in that active conservation grazing is probably unnecessary where wild grazers such as lagomorphs can have a significant beneficial impact for invertebrates.

Conclusion: Can rewilding aid Orthoptera conservation on farmland?

Intensive agriculture has significantly reduced the diversity and abundance of Orthoptera on UK farmland (Gardiner et al. 2002, Cherrill 2010, 2015). Taking less agriculturally productive land out of arable cropping and allowing it to naturally regenerate (Rewilding Max) with minimal domestic livestock grazing and only wild grazing by lagomorphs and ungulates can produce swards that are quickly colonized (c. 4–8 years) by Orthoptera species not usually found on farmland, such as *O. viridulus* or *T. undulata*. Rewilded fields should incorporate features such as old and restored ponds to provide bare earth bank habitat for groundhoppers (e.g., *T. subulata*), while ant hills develop as the grassland matures, providing exposed soil and shorter swards for basking and ovipositing grasshoppers (e.g., *C. brunneus*). Lagomorph grazing in and around ponds and ant hills enhances the value of these bare earth features by maintaining them at an early successional stage. Of course, the response is species specific, and here the heterogeneity of micro-habitat is important to cater for short (e.g., *T. undulata*) and tall grassland (e.g., *O. viridulus*) species. A patchwork of different swards may also help to promote the highest diversity of insects (Kruess and Tscharntke 2002).

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